

BOOK REVIEW: SPOTLIGHT ON THE BUGS

ANDERSEN, N. MOLLER. 1982. *The Semiaquatic Bugs (Hemiptera: Gerromorpha), Phylogeny, Adaptations, Biogeography and Classification*. Entomograph 3, Scandinavian Science Press Ltd., Christiansholms Parallelveg 2, DK 2930 Klampenborg, Denmark. 455 pages, 638 text figures, 16 black and white plates, 3 appendices (names of higher taxa + references; generic names + references; keys to families, subfamilies and genera), Danish summary, bibliography, index. Price D.Kr. 300 (c. \$33.00 USA).

This book treats the higher classification of semiaquatic bugs within the framework of phylogenetic reconstruction. Along the way, Andersen summarizes an encyclopedic knowledge about biology of gerromorphans. In addition to being essential reading for all serious students of Heteroptera, Andersen's monograph is a showcase of how to carry out and present a systematic work which deals primarily with supraspecific taxa. Anyone contemplating a biological investigation involving gerromorphans will want to begin with *The Semiaquatic Bugs*. Anyone looking for a fascinating problem to investigate about evolutionary biology of insects will find a bushelfull while reading this volume.

The six main chapters deal with (1) phylogenetic reconstruction in general, (2) phylogeny of Gerromorpha, (3) character analysis and phylogeny of the higher taxa of gerromorphans, (4) adaptations and ecological diversifications, (5) biogeography and (6) classification. Much of the original data have been used in Andersen's previous publications but they are brought together for the first time in *The Semiaquatic Bugs* and focused on larger questions of phylogenetic relationships and higher classification. In addition to an impressive stack of previous papers dealing with species level systematics of gerromorphans bugs, Andersen has published first-rate papers dealing with life history, wing polymorphism, behaviour and functional anatomy. This unusually wide range of experience is reflected in *The Semiaquatic Bugs* and the resulting perspective will make this work most useful to non-systematists. Andersen writes with attention to problems of interest to experimental and comparative biologists who have little interest in taxonomy *per se*. Andersen's firsthand experience with ecological and behavioural work allows him to insightfully interpret and synthesize data from the literature which are frequently ignored or superficially treated in systematic works.

The writing is clear and concise and Andersen's arguments are easy to follow. When interpretations are tentative and based only upon the most likely interpretation of limited information, Andersen so indicates and often suggests how the situation might be further resolved. The volume is exceedingly well illustrated with an abundance of line drawings in the author's own hand. A reader can come to appreciate the structural diversity of gerromorphans just by flipping through the pages. The plates are of uniformly high quality and photomicrographs are clearly labeled and easy to interpret. However, plates would be easier to use if the corresponding page number had been given along with the text reference. There are few typographical errors and the book is well bound, attractively produced and moderately priced. If similar standards are maintained, entomologists can look forward to future volumes in the Entomograph series with enthusiasm.

The first chapter crisply summarizes Andersen's working principles which are those of contemporary cladistics. This chapter is probably unnecessary for most systematists but, for biologists of other persuasion, it is well at place. It allows the novice to appreciate the assumptions, strengths and weaknesses of Andersen's analysis and, especially, to understand

why the treatment that follows differs from those by previous workers. And, it allows the reader to do so without becoming lost among taxa X, Y, and Z in a dark forest of theoretical cladograms.

In chapter 2 Andersen accomplishes two tasks. First, he explicitly reconstructs the ground plan for the Gerromorpha dealing with traits of eggs, nymphs and adults. An understanding of the ground plan makes subsequent discussion about polarity of character transformation series easy to follow. Second, using the ground plan, Andersen attempts to assess the relationships between gerromorphans and other stocks of Heteroptera. He ultimately agrees with Cobben (1978, *Meded. LandbHoogesch. Wageningen*, 78-5) that gerromorphans are most representative of the ancestral heteropteran stock. However, Andersen clearly establishes the monophyletic nature of the Gerromorpha and concludes that it is the probable sister group of other heteropteran lineages and not a stem group ancestral for the suborder. Among the nine shared, derived traits which define the Gerromorpha, the quadrangular mandibular lever, organization of the pretarsus and the nature of the female gynatrial complex seem most compelling.

Although the task ahead is large, Andersen's detailed discussion leaves the reader optimistic about reconstructing the phylogeny of the Heteroptera through cladistics. Andersen shows well through example that cladistic methods need not fail when confronted with detailed and often incongruent information about distribution of character states. The main lesson is that information about many character systems must be assessed simultaneously. The main working principle is parsimony, *i.e.* the amount of homoplasy (number of convergences and parallelisms evaluated in the context of their evolutionary likelihood) is minimized. Therefore, it is at the level of characters and interpretation that Andersen's phylogenetic arguments are focused. If we aim to seek the best *tentative* explanations and are willing to state and rigorously test hypotheses of cladistic relationship instead of trying to establish links of overall similarity, there are indeed grounds for optimism.

In chapter 3, Andersen summarizes the data base used directly in his phylogenetic reconstruction. This chapter makes up about one half of the text and is a detailed comparison of external and internal anatomy of individuals belonging to each of the 8 recognized families comprising the infraorder Gerromorpha. Significant variation of character states within each family is discussed and each family is diagnosed in terms of shared derived characters. Finally the inferred relationships of subgroups within each family are presented and defended.

I take a few, minor exceptions to Andersen's arguments. For example, it is not clear why a lacinate ovipositor is best interpreted as part of the gerromorphan ground plan, despite its presence in the basal mesoveliids, given that superficial deposition of eggs is also interpreted as the primitive condition for the gerromorphs. Surely some of the lacinate character of the mesoveliid ovipositor must have evolved under selection for improved ability to place eggs within plant tissue. Nor was it clear why the divided gynatrial gland was "inferred to belong to the ground plan of the Gerrinae even if it is not found in all members of the subfamily" (p. 238).

Overall, however, I found Andersen's interpretations well founded and based upon in-depth understanding of the character systems involved. His comparative work with the unique gynatrial complex and with the structure of the metasternal scent glands and associated ducts should inspire additional studies in functional morphology. Insights

obtained about relationships of the highly derived Hydrometridae through analysis of the recently discovered *Veliometra* highlight the great strengths of cladistic analysis. Despite its overall primitive character, *Veliometra* is clearly a cladistic member of the Hydrometridae and this taxon provides a critical link for sorting out the relationships of its highly derived lineage mates. Andersen's analysis of the Gerridae is crisply and brilliantly argued and it differs considerably from that presented recently by Calabrese (1980, *Misc. Publ. Ent. Soc. Am.* 11-5]. Although Andersen's conclusions appear to be based upon a more complete consideration and firsthand analysis of characters relevant to the analysis, it would have been useful had he pointed out the main differences between his results and those of Calabrese and presented explicit arguments that favor his system.

In a short discussion of gerromorphan fossils Andersen points out that the Mesozoic fossil *Engynabis tenuis* Bode may be assigned only speculatively to the Gerromorpha because the specimen does not reveal enough structural detail. Therefore, students of gerromorphan history are left with Tertiary fossils which "represent species typical of their respective groups" and allow only the conclusion that the origin of the Gerromorpha was "probably long before the Tertiary". This conclusion is compatible with the zoogeographic analysis offered in Chapter 5.

The culmination of Chapter 3 is a summary of affinities between families of semiaquatic bugs and a formal reconstruction of their phylogeny. Andersen compares his hypotheses with those advanced by previous authors and, in my opinion, shows that his analysis represents a genuine step forward in understanding. Although Andersen is a faithful cladist and translates branching sequence directly to classification, he is concerned with generation of evolutionary novelty within phyletic lines. In that spirit, Chapter 3 closes with a discussion of "derivation load" in the Gerromorpha and thereby provides an intriguing semiquantitative description of relative divergence for each family. Derivation load is calculated as the percentage of derived characters carried by each taxon and is partitioned into components reflecting (1) divergence of family ground plans from the basal gerromorphan ground plan and (2) amount of divergence encountered within each family. Data presented suggest that although the veliids and hydrometrids have undergone the greatest divergence as a consequence of radiation, other groups such as gerrids and hermatobatids made the most significant leaps in the early stages of becoming independent lineages. It is tempting to suppose that these data provide hints of the historical action of both "gradualistic" and "punctuated" speciation within a single higher taxon.

Semiaquatic bugs have adapted to life on the water surface in a myriad of fascinating ways. In the fourth chapter, Andersen discusses adaptations with respect to habitat selection, locomotion, feeding, flight ability and reproduction. The selective factors seemingly responsible for adaptive trends are identified and relevant ecological investigations are thoroughly reviewed. The adaptive themes are woven together in a scenario which describes significant events in the evolutionary history of the semiaquatic bugs. Andersen argues convincingly that the open water surface has been invaded several times by independent lineages and shows that even marine habitats have been colonized a minimum of four times.

In discussing adaptation for life on the water surface, Andersen provides a basis for isolating significant research problems in evolutionary ecology. For example, males of some tropical gerrid species come in two distinct size classes. Andersen suggests that these represent an extreme form of alternative mating tactics. A study of the genetics of sexual

selection in such a system would surely be fascinating. We also learn that almost nothing is known about factors regulating the size of gerromorphan populations although resource limitation has been often invoked as a mechanism to explain patterns of habitat selection and evolution of wing polymorphism. Andersen makes much of a switch in foraging strategy during evolution of gerromorphs. Although I am convinced that gerrids forage quite differently from their more distant relatives like mesoveliids and hydrometrids, I don't believe that categorization of the more basal families as searching predators and those which have invaded open water ambush predators is appropriate. Yes, gerrids *sometimes* orient to prey by responding to ripple signals but most pond dwelling species generally search actively to find their prey (Spence, 1981, *Ecol.* 62: 1505-14), a large percentage of which are dead arthropods. In more derived gerrid lineages found on flowing water, bugs often position themselves so that the stream acts like a conveyer belt bringing food items to their feet. However, few of the details of gerrid foraging have been worked out.

The most significant aspect of this chapter is that Andersen shows how information, which has been of traditional interest to only ecologists and behaviourists, can be fitted within the framework of phylogenetic systematics. Evolutionary biologists can do much to unravel the complex of selective factors which structure the adaptive themes seen in each lineage. And, it is encouraging that systematists like Andersen are interested in more than coarse speculation about the environmental and behavioural constraints on evolution. Systematic work done in this spirit is likely to attract interest and input from other biologists.

Chapter 5 deals with zoogeography, first with reference to vicariance and dispersal models, and then, by discussing gerromorphan diversity with respect to the major zoogeographical realms. In my opinion, the first section of this chapter was the least successful part of the book. Probably as a result of the apparent great age of gerromorphan families, few clear vicariant patterns emerge at the level of higher taxa and Andersen suggests that present distributions are best explained as reflecting primitive cosmopolitanism with subsequent extinction. A few examples of disjunct distributions of sister taxa are explained as vicariant patterns resulting from continental movement but complete analyses are not offered in this volume. The reader is also presented with examples of widespread species, especially members of *Mesovelgia* and *Microvelgia*, which have apparently undergone remarkable range expansion through dispersal. No general theme seems to emerge from the data and analysis presented.

In contrast, the second part of the chapter shows that there are interesting zoogeographical patterns to be explained. For example, the genera of Gerrinae which dominate the northern parts of the world are virtually absent from tropical regions. Faunal diversity is maximum in the tropics and Andersen discusses this empirical observation in light of most theories which have been advanced about latitudinal diversity gradients. Not surprisingly, perhaps, there are little data available to discriminate among hypotheses and most explanations seem potentially satisfactory. Although Andersen mentions that a large portion of the tropical gerromorphan fauna is made up of wingless species, he does not explicitly link this to the idea that tropical diversity has evolved in response to climatic stability. From work reviewed in the contexts of habitat selection and wing polymorphism, we know that wing loss in temperate gerrid species seems to be associated with habitat permanency. This association seems to hold in the tropics where most wingless species occupy flowing water habitats. Zera (1981, *Evol.* 35: 218-225) has shown that low

frequencies of winged individuals in populations of *Gerris remigis* are associated with evolution of genetically divergent local populations. In the climatically stable tropics, wingless and concomitant genetic isolation could well lead to increased rates of speciation.

The last chapter provides a historical review of the classification of Gerromorpha bugs, presents Andersen's new views and briefly characterizes the Gerromorpha with respect to numbers of genera and species. Andersen includes Gerromorpha taxa in four superfamilies: (1) Mesoveliodea, (2) Hebroideia, (3) Hydrometroideia and (4) Gerroideia. The chief innovations are recognition of the families Paraphrynoveliidae and Macroveliidae as cladistic members of the Hydrometroideia, the hebrids are seen to be more closely related to the rest of the Gerromorpha than to the mesoveliids, and the madeoveliids are included in the Mesoveliidae. These changes are consistent with Andersen's phylogenetic analysis and seem to be well advised. The chapter also provides a sound basis for organizing the families into subfamilies and tribes. Keys given in appendix III allow identification of the known genera of semiaquatic bugs of the world. The keys worked well for the genera that I had on hand in my collection.

This book is a refreshing exodus from theory bound systematics. However, the study also goes far beyond the usual fare of taxonomic description and evolutionary speculation and grapples with data of interest to a broad range of biologists. As a result, the treatment will stand as a milestone in the study of semiaquatic bugs, even as new trends emerge in theoretical systematics. I attribute the success of this volume to two main factors. First, as a higher taxon, the Gerromorpha includes an unusual amount of structural and lifestyle diversity packaged in a manageable number (c. 1300) of species worldwide. Thus, a treatment can be simultaneously detailed and wide ranging. Second, the spotlight is on the bugs which are obviously Andersen's first academic love. If the book is widely read, and I hope it will be, those of us working on semiaquatic bugs should soon have lots of company.

John R. Spence
Department of Entomology
University of Alberta

